SUBDIVISIONS OF THE GENUS *PTILINOPUS* (AVES, COLUMBAE)

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SYNOPSIS

Previous arrangements of the species of *Ptilinopus* result in unnatural groupings. When one abandons the attempt to provide diagnoses for all groups, and gives due weight to the facts of geographical distribution, a far more natural classification can be constructed.

INTRODUCTION

THE genus *Ptilinopus* contains a large number of brightly coloured fruit-pigeons distributed from the Malay Peninsula, Philippines and Marianas to New South Wales, the Marquesas, and Henderson Island. Even within obviously natural groups of species of this genus so much interspecific variation occurs that it is almost impossible to find diagnostic characters. The last comprehensive review with diagnoses is that by Salvadori (1893) which, as was usual at that period, ascribes exaggerated importance to so-called anatomical characters. Some species have been reviewed by Rensch (1929), Mayr (1940), Ripley and Birckhead (1942) and Amadon (1943), but no general survey has appeared, except that Peters (1938) reviewed the limits of the genera of fruit-pigeons and gave diagnoses for those

genera he recognized, together with a very brief survey of the interrelations of species within each genus. The checklist given by Peters (1937) is good for subspecific ranges and synonymy, but the arrangement of the species is unfortunate, several closely related forms being separated widely. Also, no indication is given of the limits of superspecies or species-groups.

The purpose of this paper is to present a classification of these pigeons, based on a study of the collections in the British Museum (Natural History). I am deeply indebted to Mr. J. D. Macdonald, who has given me every facility in examining the specimens, and to Mr. R. E. Moreau for advice and criticism.

PRINCIPLES

(1) *Recognition of natural groups*

If each of the members of a group of species is more closely related to some other members than to any species outside it, the group is natural; but it may well happen that every character that is confined to the group and therefore might be proposed as diagnostic is lost or modified in one or more species. If those species are clearly related by all their other characters to the rest of the group, they cannot be excluded from it.

This is the state of affairs found in the genus *Ptilinopus*. Consequently, the descriptions given below must be understood as indicating general characteristics, not as rigidly defining each subdivision. As Peters (1938) remarked of the subgenus *Ptilinopus*, it is very difficult to draw up a diagnosis that applies to all the species. I would add that it is unnecessary. When a natural group can be recognized but not diagnosed as such, it is sufficiently indicated by a description and a list of the contained species, as in the present paper.

When two species are clearly very closely allied but differ in one conspicuous character, it is obvious that in respect to these two species this character is only of specific importance. In another group, its distribution may coincide with that of so many other characters that it can be cited as characteristic of a genus, family, or group of even higher rank. The test of taxonomic importance of any character in a particular group is its distribution in that group with respect to all other characters.

This statement is true whatever the nature of the character—anatomical, physiological, embryological, genetical or ecological. The remark of Manuel (1936*b*) that " The subfamily Ptilopodinae is an artificial group for the reason that there are no trenchant structural characters peculiar to it " is consequently unacceptable. In some natural groups of birds the beak, feet, or structure of the feathers may show extraordinary variability while the colour pattern remains very constant; in others, the reverse is true. Consequently there is no need to assume *a priori* that in any group of birds structure is always more important taxonomically than colour-pattern. This was very nearly the assumption made by Salvadori (1893) as of course by most authors of that time. Consequently his keys almost always begin with an " anatomical " character (emargination of the first primary, length of the tail and wing, or strength of the beak). Unfortunately these characters are not invariably of the highest importance in *Ptilinopus* and its allies, and Peters (1938),

although he implies (p. 376) that external structural characters are a *sine qua non* for erecting a subfamily (which may be true in practice but cannot be made into an absolute rule), remarks of *Ptilinopus* and its allies that " On the whole, colour in this group seems just as important, if not more so than structure." A survey of all the species, originally made without reference to Peter's paper, confirms his opinion.

(2) *Size*

The importance of any character, as was shown above, is determined only by its distribution in any particular group with respect to all other characters, and no one class of characters can be regarded on principle as always of greater taxonomic importance than any other.

Equally, no one class of characters can be considered on principle as always useless. Size tends to vary greatly in birds both between and within species, and is therefore not usually of much taxonomic value in groups above the level of the species. However, in the genus *Ptilinopus* size tends to remain comparatively constant in the species of some groups. The subgenera *Leucotreron* and *Ramphiculus* contain species which, for the genus, are rather or very large (wing-length 150–170 mm.). In the subgenus *Ptilinopus* all the members of the ornatus species-group ((10)–(14)) are rather large for this subgenus (wing-length 135–160 mm.), while those of the purpuratus species-group ((15)–(30)) with a solitary exception (*Pt. huttoni* (26)) are rather small (wing-length 95–145 mm.). Size is therefore included as a character in the descriptions of the groups. Within the genus as a whole wing-lengths of 90–139 mm. are considered small, 140–159 medium, and 160–170 large.

(3) *Keys and natural classifications*

Keys are constructed for the rapid identification of specimens. The characters employed are therefore those that are readily discernible, present in the largest possible number of individuals (not confined, for example, to a fleeting stage of development), least variable in their expression, and most easily defined verbally.

" Natural " classifications, on the other hand are constructed to display the general affinities and presumed evolutionary interrelationships of different forms. For this purpose characters totally different from those used in a key to the same group may be chosen, since the conspicuousness of a character bears no direct relationship to its taxonomic and phylogenetic importance. Yet monographs are still often burdened with " keys " which are designed to act both as guides to identification and as succinct accounts of a natural classification. In such " keys " it is common to find not only that the characters employed are often of little practical use for identification, but also that the necessity for defining each group by one or two characters may actually prevent the recognition of such natural groups as those described immediately above, which have no diagnostic characters. The reason why such " keys " are constructed is, of course, that by using them a new and undescribed form can usually be put into its natural group, whereas in a key made solely for identification it may very well be associated with widely differing

species with which it happens to have some unimportant but conspicuous character in common. (For example, the character " bifid breast feathers " would bring together *Pt. porphyrea* (s.g. *Leucotreron*) and *Ducula goliath*, and most of the purpuratus species-group of *Ptilinopus*.) Nevertheless, the practice of combining both functions in the same key is not good. Together with the assumption that structure is always more important than colour, it was responsible for some of Salvadori's least successful groupings in *Ptilinopus*, as can be readily verified by anyone who will work through his classification. However, it is a striking tribute to Salvadori's genius that although he worked under these unnecessary limitations, his classification was by far the best produced until then, and most of his groups can still be regarded as natural.

(4) *Use of species-groups and subgenera*

Mayr (1942 : 290) has pointed out the great taxonomic advantages of the species-group. It is an informal natural group of closely related species, below the rank of a subgenus, the recognition of which involves no complication of the scientific names of the species contained in it. Moreover, having (unlike the subgenus) no formal name, it is not readily raised to the rank of a genus with a consequent change of the generic name throughout its component forms. In addition, in *Ptilinopus*, its use permits the recognition of natural groups of species without a general promotion of the subgenera to genera, and the genus perhaps to a subfamily. By using species-groups, the generic name can be retained throughout (which indicates the close relationship of the included species) while unmanageably large groups of species can nevertheless be broken up.

As the species-group is burdened by no formal rules there is no necessity to use the oldest valid name within a group as the name of that group. Consequently the group containing as its oldest named form the very atypical *Pt. tannensis* (14) can be called the ornatus group after a much more typical member (12). I have not changed the name of the purpuratus species-group (Ripley & Birckhead, 1942) because one should avoid nomenclatural disturbances wherever possible, and *Pt. purpuratus* (27), although a very simplified form, is certainly a member of the species-group that bears its name.

Although the subgenus has the disadvantage that it lengthens the names of its component forms in full citations, and is a standing temptation to reviewers to raise it to generic rank, it is nevertheless useful when, as in the genus *Ptilinopus*, many species-groups must be recognized but they fall clearly into two or more groups within the genus. Consequently it is used here to distinguish the three very natural groups which the genus *Ptilinopus* comprises. In smaller or less heterogeneous genera the species-group should be sufficient, without the use of subgenera.

(5) *The superspecies*

The superspecies (Mayr, 1942 : 169) is a monophyletic group of forms which replace each other geographically but are too diverse for all to be ranked as sub-

species of a single species. The limit of permissible diversity cannot of course be specified, since in some groups good species are very similar, in others extremely diverse, so that in the former the diversity permissible among subspecies of a single species will be much less than in the latter, and forms with striking characters will be unhesitatingly separated as distinct species. Mayr (1942) gives examples of monophyletic arrays of geographical representatives in which some forms have even been segregated into a separate genus. Consequently a single superspecies may include only a few species of a single species-group, as in the occipitalis species-group ((4)–(7)), or all of them as in the lechlancheri species-group ((8)–(9)), or all of one species-group and one or more of another, as, for example, in the genus Halcyon (Mayr, 1942).

Consequently, the superspecies cannot strictly be used as a rank in the taxonomic hierarchy. However, when a series of geographically replacing forms is very heterogeneous there is usually some doubt as to whether it is really monophyletic, and it would be unwise, therefore, to list it as a superspecies. If there is no doubt, then most workers would consider that, since geographical variation is considerable in this series, the limits of subgeneric and generic variation in the natural group containing it should be wide. Consequently it would be given a low rank in the hierarchy. As a result it is rare to find a superspecies that transgresses the limits of a species-group, and in practice the superspecies can be regarded as a rank between the species and the species-group. The hierarchy of ranks used in the following classification is therefore :

Genus,
Subgenus,
Species-group,
Subgroup (of species-group),
Superspecies,
Species.

CLASSIFICATION

The proposed classification is illustrated by the diagrams (Figs. 1 and 2) in which are represented all the species recognized by me. These diagrams are intended to demonstrate only the plumage pattern of each species. Relative size is not given and in each species the most highly ornamented subspecies and sex are shown (except in *Pt. rivoli* (32) and *solomonensis* (31) where there is very confusing convergence). Each species is given the same number in the diagrams as in the classification. Cross-hatching is used to represent shades of red, from orange to purple. All other colours are represented by stippling of appropriate darkness. Except for *Pt. merrilli* (5), specimens of all species and nearly all subspecies have been examined. The diagram of *Pt. merrilli* is based on the coloured plate of *P. m. faustinoi* given by Manuel (1936*a*), and on the descriptions by Delacour and Mayr (1946) and McGregor (1916). Full references to original descriptions of all forms will be found in Peters (1937) and Salvadori (1893).

(1) *Brief list*

Genus *Ptilinopus*

Subgenus *Leucotreron*

Pt. cincta superspecies
Pt. porphyrea (1)
Pt. dohertyi (2)
Pt. cincta (3)

Subgenus *Ramphiculus*

(*a*) Occipitalis species-group

(i) Marchei subgroup

Pt. marchei (4)
Pt. merrilli (5)

(ii) Occipitalis subgroup

Pt. occipitalis superspecies
Pt. occipitalis (6)
Pt. fischeri (7)

(*b*) Leclancheri species-group

Pt. leclancheri superspecies
Pt. leclancheri (8)
Pt. subgularis (9)

Subgenus *Ptilinopus*

(*a*) Ornatus species-group

(i) Wallacii subgroup

Pt. wallacii (10)
Pt. aurantiifrons (11)

(ii) Ornatus subgroup

Pt. ornatus (12)
Pt. perlatus (13)

(iii) Tannensis subgroup

Pt. tannensis (14)

(*b*) Purpuratus species-group

(i) Superbus subgroup

Pt. superbus superspecies
Pt. superbus (15)
Pt. perousii (16)

(ii) Purpuratus subgroup

Pt. monacha (17)
Pt. coronulatus (18)
Pt. pulchellus (19)
Pt. regina (20)
Pt. roseicapilla (21)
Pt. greyii (22)
Pt. richardsii (23)
Pt. porphyraceus (24)

Pt. rarotongensis (25)
Pt. huttoni (26)
Pt. purpuratus (27)
Pt. insularis (28)
Pt. mercieri (29)
Pt. dupetithouarsii (30)

(*c*) Viridis species-group
(i) Rivoli subgroup

Pt. solomonensis (31)
Pt. rivoli (32)

(ii) Viridis subgroup

Pt. viridis (33)

(*d*) Hyogastra species-group
(i) Iozonus subgroup

Pt. iozonus superspecies
Pt. iozonus (34)
Pt. insolitus (35)

(ii) Hyogastra subgroup

Pt. hyogastra superspecies
Pt. hyogastra (36)
Pt. granulifrons (37)
Pt. naina (38)
Dubious member of this superspecies
Pt. melanospila (39)

(*e*) Jambu species-group

Pt. jambu (40)

(*f*) Lutovirens species-group

Pt. luteovirens superspecies
Pt. victor (41)
Pt. luteovirens (42)
Pt. layardi (43)

(2) *Detailed classification*

Genus *Ptilinopus* Swainson, 1825

Medium to small fruit-pigeons (wing-length 170 to 90 mm.) almost always with a plumage pattern including well-defined patches of colour forming conspicuous ornaments on the head and underparts, without a conspicuous yellow stripe on the wing, and with the first primary usually more or less clearly emarginate (falcate) at the distal end.

Subgenus *Leucotreron* Bonaparte, 1854 (Fig. 1).

Rather large Ptilinopids (wing-length about 160 mm.), with the head, neck, mantle and breast concolorous or simply patterned in bright colours and sharply marked off

from the rest of the body by a narrow pale line followed on the ventral surface by a dark transverse bar. No tendency to ornamentation of the wings. First primary emarginate. Greater and Lesser Sunda Isles, Australia.

(1) *Pt. porphyrea* (Temminck, 1823). Sumatra, Java, Bali.
(2) *Pt. dohertyi* (Rothschild, 1896). Sumba.
(3) *Pt. cincta* (Temminck, 1810). Lesser Sunda Isles except Sumba, from Bali to Teun, Damar and Babar, and Northern Territory of Australia.

These three species are very closely allied, and if the very small overlap of *Pt. porphyrea* and *cincta* on Bali may be disregarded, they can be grouped as the *Pt. cincta* superspecies.

Subgenus *Ramphiculus* Bonaparte, 1854 (Fig. 1)

Medium-sized to large Ptilinopids (wing-length 150 to 170 mm.) with the most deeply coloured patches of the head-ornamentation (excepting the chin-stripe) lateral, sometimes meeting on the hind neck to form a ring. (A red cap occurs in *Pt. merrilli faustinoi*.) No tendency to ornamentation of the wings, nor to a pale line bounding the whole of the anterior parts as in *Leucotreron*. First primary emarginate, usually very obviously. Philippines and Celebes.

(*a*) Occipitalis species-group

Rather highly ornamented forms (plus one with a simplified pattern, *Pt. merrilli*), with a complex pattern on the head in which a chin stripe is not a well-marked feature, with breast and belly usually of different colours separated by a dark transverse abdominal line or band, and with spotted under tail coverts.

(i) Marchei subgroup

With a red cap and black auriculars, or only a cap, or no ornamentation on the head. Outer web of the secondaries composed of short widely separated red barbs.

(4) *Pt. marchei* (Oustalet, 1880). Philippines ; Luzon and Polillo.
(5) *Pt. merrilli* (McGregor, 1916). Philippines ; Luzon and Polillo.

(ii) Occipitalis subgroup.

With a red or black band joining the red auriculars across the nape. One superspecies.

(6) *Pt. occipitalis* G. R. Gray, 1844. Philippines.
(7) *Pt. fischeri* Brüggemann, 1876. Celebes.

(*b*) Leclancheri species-group

Rather plain species with a well marked dark chin-stripe, and plain (unspotted) brown under tail coverts. One superspecies.

(8) *Pt. leclancheri* Bonaparte, 1855. Philippines.
(9) *Pt. subgularis* Meyer and Wiglesworth, 1896. Celebes, Peling, Banggai and Sula Mangoli.

Subgenus *Ptilinopus*

Small to medium Ptilinopids (wing-length 90 to 160 mm. only in *Pt. huttoni* (26) 170 mm.), with strong tendencies to ornamentation of the wing coverts and scapulars and of the underparts, either a pectoral or abdominal patch or both being almost always present. The most deeply coloured patches on the head (excepting the chin stripe) are dorsal and median, forming a cap. First primary often clearly emarginate, sometimes obscurely so or merely tapering to the tip. Principally the New Guinea region and islands to the eastwards.

(*a*) Ornatus species-group

Forms rather large for this subgenus (wing length 135–160 mm.), highly ornamented (except for *Pt. tannensis* (14), an isolated form with a simplified pattern). Wing coverts spotted with pink, grey or white. There is a strong tendency to grey or olive yellow on the neck and breast. Abdomen plain green or with only a pale abdominal patch. Abdominal spot or bar (dividing the abdomen from the breast) always absent. Under tail coverts spotted. First primary not or only very slightly emarginate.

(i) Wallacii subgroup

With a red or orange cap, grey-spotted wing coverts, white chin and cheeks, and grey breast.

(10) *Pt. wallacii* (G. R. Gray, 1858). Babar, Timorlaut, Kei and Aru Isles.

(11) *Pt. aurantiifrons* (G. R. Gray, 1858). New Guinea, Western Papuan Islands, and Aru Isles.

(ii) Ornatus subgroup

With an olive-yellow cap (red in one subspecies), a grey chin, and olive-yellow breast. Wing coverts spotted with grey or bright pink.

(12) *Pt. ornatus* (Schlegel, 1871). New Guinea.

(13) *Pt. perlatus* (Temminck, 1835). New Guinea.

(iii) Tannensis subgroup

Head olive-yellow, most of the rest of the body plain green. Scapular spots white. Related to the ornatus subgroup.

(14) *Pt. tannensis* (Latham, 1790). New Hebrides and Banks Islands.

(*b*) Purpuratus species-group

Small to medium species (wing-length 95 to 145, 170 in *Pt. huttoni* (26)) with a bright red, purple or blue cap bordered behind with yellow (or with vestiges of such a cap), and with clearly or obscurely bifid breast-feathers. Scapular and wing-covert spots present, dark blue, pink, pale purple, or emerald green, often not clearly marked. Abdomen ornamented with a large patch and a darker transverse bar or spot, reduced or absent in a few forms. Under tail coverts plain red, orange or

yellow (spotted only in *Pt. superbus*). First primary emarginate, almost always very clearly.

(i) Superbus subgroup

Lower neck and upper back with a more or less extensive bright brownish red or dark red band. Wide transverse abdominal band present. One superspecies.

(15) *Pt. superbus* (Temminck, 1810). Celebes and the Sulu Archipelago to the Solomons and eastern Australia.

(16) *Pt. perousii* Peale, 1848. Fiji, Tonga and Samoa.

(ii) Purpuratus subgroup

With no red on the lower neck and upper back, and no distinct humeral patch on the wing. With a narrow abdominal band transversely elongated (*Pt. pulchellus* (19)) or, much more frequently, a rounded or longitudinally elongated abdominal spot. One superspecies with two doublets (see p. 283).

(17) *Pt. monacha* (Temminck, 1824). North Moluccas (Halmahera, Ternate Batjan).

(18) *Pt. coronulatus* (G. R. Gray, 1858). New Guinea, Japen, Salawati and Aru Isles.

(19) *Pt. pulchellus* (Temminck, 1835). New Guinea and Western Papuan Islands.

(20) *Pt. regina* Swainson, 1825. Eastern and northern Australia, eastern Lesser Sunda Isles, Banda and Kei Isles.

(21) *Pt. roseicapilla* Lesson, 1831. Marianas.

(22) *Pt. greyii* Bonaparte, 1857. New Caledonia to Santa Cruz Islands and Gower Island.

(23) *Pt. richardsii* (Ramsay, 1882). Ugi, Santa Anna, and Rennell Island (Solomons).

(24) *Pt. porphyraceus* (Temminck, 1821). Fiji, Tonga, Samoa, Caroline and Palau Islands.

(25) *Pt. rarotongensis* Hartlaub and Finsch, 1871. Rarotonga.

(26) *Pt. huttoni* (Finsch, 1874). Rapa Island.

(27) *Pt. purpuratus* (Gmelin, 1789). Society Isles and Tuamotu or Lau Archipelago.

(28) *Pt. insularis* (North, 1908). Henderson Island.

(29) *Pt. mercicri* (Des Murs and Prévost, 1849). Nukuhiva and Hivaoa (Marquesas).

(30) *Pt. dupetithouarsii* (Neboux, 1840). Marquesas, widespread.

(c) Viridis species-group

Forms medium sized for this subgenus (wing-length 115–135 mm.). Pectoral patch large, sharply defined and coloured white, yellow, or deep red. Abdominal patch reduced and dark purple, or absent. Wing-covert spots present, dark blue or grey. First primary not or only very slightly emarginate.

(i) Rivoli subgroup

Wing spots dark blue. Abdominal patch present. Red or purple cap present, sometimes reduced to a pair of supraloral spots. Under tail coverts yellow.

(31) *Pt. solomonensis* (G. R. Gray, 1870). Solomon Islands, Bismarck Archipelago and some islands in Geelvink Bay.

(32) *Pt. rivoli* (Prévost, 1843). South Moluccas, Western Papuan Islands, north-west New Guinea, islands in Geelvink Bay, some islands off south-eastern New Guinea, Solomon Islands.

(ii) Viridis subgroup

Wing spots grey. Abdominal patch and red cap absent. Head shades of green and grey (rarely white). Size of pectoral patch varies greatly. Under tail coverts spotted.

(33) *Pt. viridis* (Linnaeus, 1766). South Moluccas, Western Papuan Islands, north-west New Guinea, islands in Geelvink Bay, some islands off south-eastern New Guinea, Solomon Islands.

(*d*) Hyogastra species group

Forms medium-sized to small for this subgenus (wing-length 90–130 mm.). Breast, neck and back plain green, unornamented. Abdomen with an orange or violet patch (absent in *Pt. melanospila* (39)). Head plain green or grey, unornamented or with a chin stripe and nuchal spot. First primary indistinctly emarginate or merely tapering.

(i) Iozonus subgroup

Head green with greyish ill-defined chin stripe. Abdominal patch large, orange. Grey patch on bend of wing, grey spots on wing-coverts. Under tail coverts spotted. One superspecies.

(34) *Pt. iozonus* (G. R. Gray, 1858). New Guinea, Western Papuan Isles and Aru Isles.

(35) *Pt. insolitus* (Schlegel, 1863). Bismarck Archipelago.

(ii) Hyogastra subgroup

Head grey (green in *Pt. naina*). Abdominal patch violet (absent in *Pt. melanospila*). Under tail coverts yellow, or yellow grading to red, not spotted. One superspecies. (Possibly *Pt. melanospila* should be kept separated.)

(36) *Pt. hyogastra* (Temminck, 1824). Halmahera and Batjan (North Moluccas).

(37) *Pt. granulifrons* Hartert, 1898. Obi Major.

(38) *Pt. naina* (Temminck, 1835). New Guinea and Western Papuan Isles.

(39) *Pt. melanospila* (Salvadori, 1875). Philippines, Celebes, Java, Lesser Sunda Isles (Bali to Alor) and Ceram.

(*e*) Jambu species group

Head red with black chin stripe. Upper parts green, underparts white with a pink flush on the upper breast and brown under tail coverts. First primary emarginate.

(40) *Pt. jambu* (Gmelin, 1789). Malay Peninsula, Sumatra, Borneo and islands between.

(*f*) Luteovirens species group

Rather small forms (wing-length about 115 mm.). Head more or less olive-yellow, rest of body almost uniform green, orange or yellow, with no colour-ornaments. Some contour feathers lax and hairy or bifid, or long and thickened. First primary not emarginate. One superspecies, confined to Fiji.

(41) *Pt. victor* (Gould, 1872). Vanua Levu, Taviuni, Kio Rambi, Ngamea, Lauthala.

(42) *Pt. luteovirens* (Hombron and Jacquinot, 1841). Viti Levu and nearby islands.

(43) *Pt. layardi* (Elliot, 1878). Kandavu and Ono.

NOTES ON THE CLASSIFICATION

(1) *Generic and subgeneric limits*

Peters (1938) divides the species considered in the present paper into three genera, *Leucotreron* (i.e., the subgenera *Leucotreron* and *Ramphiculus*), *Ptilinopus* (the subgenus *Ptilinopus* without the luteovirens species-group), and *Chrysoena* (the luteovirens species-group), which is divided into two subgenera. In this he differs from Salvadori only in promoting *Leucotreron* from a subgenus of *Ptilinopus*, and removing *Pt. jambu* (40) from it, in using no subgenera of *Ptilinopus* (Salvadori recognized twelve), and in accepting Wetmore's subdivision of *Chrysoena* (1925 : 833). Amadon (1943) has shown conclusively that *Chrysoena* must be ranked as a single superspecies (41–3), which requires no subdivision, of *Ptilinopus*. The separation of *Leucotreron* is justifiable since it differs sharply from the other groups recognized as subgenera of *Ptilinopus* by Salvadori, but when these are ranked only as species-groups, there is no good reason why *Leucotreron* should be generically separate. Moreover, as the classification given above will show, *Leucotreron* itself requires division. A glance at the diagrams indicates that the major division of the genus is into three, not two, groups, which have very different colour patterns and distributions ; accordingly, all three are recognized here as subgenera. This arrangement is the more satisfactory since the colour pattern of the subgenus *Leucotreron*, as recognized here, is so like that seen in both *Drepanoptila* (as Peters recognized) and in some of the most ornamented species of *Ducula*, that a complete revision of all the fruit pigeons may possibly show that *Leucotreron* should be separated generically from *Ramphiculus* and *Ptilinopus*.

The characters by which both Peters and Salvadori define their group *Leucotreron* (i.e., *Leucotreron* plus *Ramphiculus*) are the relatively long tail and the absence of a sharply-defined red or violet cap. Peters adds that the tarsus is feathered for more than half its length, there are no spots on the scapulars, tertials or wing coverts, and a humeral patch is absent, and refers *Pt. jambu* (40) not to *Leucotreron* but to *Ptilinopus*. In all these forms, the length of the tail tends to be associated directly with body size, which can vary considerably within a single species-group. The feathering of the tarsus is variable, but it is true that it is on the whole more extensive in both *Ramphiculus* and *Leucotreron* than in *Ptilinopus*. All the other characters are negative. Consequently, what *Ramphiculus* and *Leucotreron* share is mainly medium to large size and the absence of the distinctive characters of *Ptilinopus*. On such grounds as these it is difficult to see why *Ptilinopus* and *Leucotreron* should not be combined instead, in opposition to *Ramphiculus*, an arrangement which has never yet been proposed ; but even a cursory inspection of the positive characters of *Leucotreron* and *Ramphiculus* shows that all these subgenera must be separated.

The only species difficult to place is *Pt. jambu* (40), which shows an extraordinary mixture of characters. Because of its brown under tail coverts and black chin stripe Salvadori associated it with *Pt. leclancheri* (8) and *subgularis* (9), its emarginate first primary, lack of a cap, and rather long tail being sufficient to include it in his *Leucotreron*. Peters merely remarks that by his definitions it is a *Ptilinopus* (1938 : 378), but it is not easy to understand this remark, since his diagnosis of *Ptilinopus* is " tail less than seven-tenths of wing, often less than six-tenths, usually a trifle over six-tenths ; tarsus never feathered for more than three-quarters of its length, seldom over one-half ; a sharply-defined red or violet cap ; spots on scapulars, wing-coverts or tertials ; bend of wing often differently coloured from the back," while for his *Leucotreron* he gives " tail more than seven-tenths length of wing (usually more than 75 per cent.) ; tarsus feathered for more than half its length (usually from three-quarters to completely) ; no sharply-defined red or violet cap ; no spot on scapulars, wing coverts or tertials ; bend of wing concolour with back (no humeral patch)."

In fact, the curious distribution of red on the head of *Pt. jambu* could be derived either by extension of the red cap (and sometimes malar spots) of some *Ptilinopus* or by reduction of the pattern found in either *Leucotreron* or *Pt. marchei* (4). The chin stripe, unicolorous under tail coverts, pale underside, and lack of wing-ornaments are very reminiscent of *Ramphiculus* (the leclancheri species-group) but also, except for the pale underside, of *Pt. melanospila* (39) (*Ptilinopus*, hyogastra species-group). The distribution could be the result of a westward invasion from Celebes by either of these species-groups, or indeed of an extension from Borneo or Malaya by a geographical representative of *Pt. porphyrea*, producing a double invasion of Sumatra.

Garrod (1874) states that *Pt. jambu* (40), *Pt. perousii mariae* (purpuratus species-group (16)) and *Pt. melanospila melanauchen* agree in the structure of the gizzard and differ from *Treron calva*. Cadow (1933) who corrects and extends Garrod's observations, compared *Pt. cincta* (3), *porphyrea* (1) and *dohertyi* (2) (all *Leucotreron*) and *Pt. jambu* (40) with species of *Megaloprepia, Ducula, Treron, Columba*, and

Didunculus. He concluded that three main types of gizzard could be distinguished in the fruit pigeons, and that *Pt. jambu* agreed in this respect with the sub-genus *Leucotreron*. It seems, therefore, that the structure of the gizzard is much the same within the genus *Ptilinopus*, in the subgenera *Leucotreron* and *Ptilinopus*, and in *Pt. jambu*, and consequently gives no information about the position of *Pt. jambu*.

On the whole, the characters of *Pt. jambu* seem to me to suggest an association with *Pt. melanospila* (39) and thence with the rest of the subgenus *Ptilinopus*, but I have placed it in a species-group of this subgenus only with the greatest hesitation. It is most remarkable that the species situated geographically at the point of convergence of the ranges of the subgenera of *Ptilinopus* should show such a mixture of the characters of all three.

(2) Leucotreron *and* Ramphiculus

In discussing the species of these two subgenera Peters (1938 : 378) was misled by the bifid breast feathers of *Pt. porphyrea* (1) and the rich red on its head and breast into considering it most closely allied to the subgenus *Ptilinopus*, and to *Pt. occipitalis* (6) and *Pt. marchei* (4), the most ornamented members of *Ramphiculus*. Consequently he proposed an artificial arrangement beginning with *Pt. porphyrea* (1), followed by the occipitalis species-group (4–7), then the leclancheri species-group (8–9), and finally *Pt. cincta* (3) and *dohertyi* (2) which he regarded as highly specialized. " The more I study *cinctus* and *dohertyi*," he writes, " the more apparent it becomes that these two species are the most specialized members of the genus [his *Leucotreron*] ; it is also evident that in spite of their superficial dissimilarity to each other in colour, they are certainly derived from the same ancestral stock, the densely feathered tarsi, proportion of wing to tail, modification of the inner primaries and the pale anterior part of the body sharply defined from the dark posterior, all point to some common ancestor." His failure to associate them with *Pt. porphyrea* in spite of these very apposite remarks is in agreement with the fact that in the Checklist (1937) he arranged the members of the purpuratus species-group in a very similar and artificial way, bringing together the most highly ornamented forms with no regard for the geographical evidence.

Bifid breast-feathers occur independently (as Peters points out, p. 388) in several groups of pigeons, including (to take examples only from the fruit-pigeons) species of the purpuratus species-group and luteovirens species-group in the subgenus *Ptilinopus*, and *Ducula goliath*. They vary much in degree of development even among closely related forms ; even if they do represent the retention of an ancestral character, it is evident that the common ancestor possessing them must be a long way back in the lineage of the pigeons. Certainly those species that possess them to-day are not closely related. The whole pattern of ornamentation of *Pt. porphyrea* links it not with the subgenera *Ramphiculus* or *Ptilinopus*, but with *Pt. dohertyi* and *Pt. cincta*.

Even if richness of ornamentation can be considered as one " character," it is not a useful character in this genus since it has evidently been lost (or perhaps gained) independently several times, as shown in the following table :

Ornamentation in Closely Allied Species

Species-group.	Complex.	Simple.
Occipitalis . .	*Pt. marchei* (4)	*Pt. merrilli* (5)
	Pt. occipitalis (6)	*Pt. fischeri* (7)
	Pt. leclancheri (8)	*Pt. subgularis* (9)
Ornatus . .	*Pt. ornatus* (12) and *perlatus* (13)	*Pt. tannensis* (14)
Purpuratus . .	*Pt. superbus* (15)	*Pt. perousii* (16) (see Cain, 1954)
	Pt. regina (20)	*Pt. purpuratus* (27) and geographically adjacent forms.

The luteovirens species-group (41–3) also consists entirely of a group of long-isolated forms with extremely simple patterns derived from the subgenus *Ptilinopus* (Amadon, 1943) which contains principally highly ornamented forms. Variation between a complex and a more simple pattern has therefore occurred at least seven times independently in the genus (and certainly involves a simplification in three examples). But, more important, " richness of ornamentation " as a character is clearly applicable to species which agree only in that they are richly ornamented and differ profoundly in their patterns of ornamentation. *Pt. porphyrea* (1), *marchei* (4) and *superbus* (15), for example, are all richly ornamented, but their affinities are not with each other but with *Pt. dohertyi* (2), *merrilli* (5) and the purpuratus species-group (15–28) respectively ; to class them together on the basis of this very superficial " character " is to ignore entirely the wealth of evidence on their real affinities provided by their pattern of ornamentation. Colours often vary greatly in intensity between subspecies, still more between species, but the pattern tends to remain constant in most species-groups. There is no doubt that the pattern of *Pt. porphyrea* (1) links it with *Pt. dohertyi* (2) and *Pt. cincta* (3).

The three species of *Leucotreron* are geographical representatives except for a single overlap on Bali, and can be regarded as a single superspecies. The loss of bright red pigment in the Lesser Sunda Isles form (*Pt. cincta* (3)) is paralleled by the reduction of red and yellow in the subspecies of *Pt. regina* (20) (purpuratus species-group) in the same area. No other species of the genus *Ptilinopus* is found, in these islands except *Pt. melanospila* (39), which is obviously a very recent arrival from Celebes.

The species of *Ramphiculus* fall naturally into two ecological groups, the marchei subgroup (4–5) being confined to mountain forest in the Philippines (Delacour and Mayr, 1946), while *Pt. occipitalis* (6) and *lechlancheri* (8) are lowland-forest species both of which have colonized Celebes and produced there simplified forms with no ornamentation on the breast and belly.

(3) *Subgenus* Ptilinopus

This subgenus can be readily subdivided into five species-groups, characterized by the accentuation of different elements of the pattern. In the ornatus group

there is considerable ornamentation of the wing-coverts and head, but very little on the lower breast and belly. In the purpuratus group the cap, breast-patch, abdominal band or spot, and abdominal patch are conspicuous. In the viridis group the breast-patch is greatly accentuated, and in the hyogastra group the abdominal patch. The luteovirens species-group (41–3), like *Pt. perousii* (16) (Cain, 1954) shows a simplified pattern, as is usual in members of reduced avifaunas.

Strong sexual dimorphism is found sporadically in the subgenus *Ptilinopus* (but in the other subgenera only in *Pt. leclancheri* (8)) and requires discussion in relation to specific limits. It occurs in the ornatus group only in *Pt. tannensis* (14) (Amadon, 1943). In the purpuratus group it is present in both members of the superbus subgroup, and in *Pt. monacha* (17), which is otherwise very closely related to *Pt. coronulatus* (18). In the hyogastra group dimorphism is slight or absent except in *Pt. melanospila* (39) in which the female has a green head. It is also seen in *Pt. jambu* (40) in which the red of the head is much duller in the female and there is some green on the breast. In the viridis group strong dimorphism is usual, but it varies greatly in the various subspecies of *Pt. viridis* (33). In this species there is a red breast-patch, which is large in *Pt. v. viridis* (southern Moluccas) and present in both sexes although perhaps very slightly smaller in the females. In *Pt. v. pectoralis* (western Papuan Islands and north-west New Guinea) it is very small in the males and absent in the females. In *Pt. v. salvadorii* (Japen and the adjacent part of northern New Guinea) it is rather larger and is present, though reduced, in the females. In fact it appears that in these subspecies the patch is always smaller in the females than in the males and when it is very reduced in the males it is necessarily absent in the females. But in *Pt. v. geelvinkianus* (some islands in Geelvink Bay) it is large in the males and quite absent in the females. In *Pt. v. vicinus* (D'Entrecasteaux Archipelago and Trobriand Isles), *Pt. v. lewisii* (Lihir Islands and most of the Solomons), and *Pt. v. eugeniae* (San Christobal) it is quite large in both sexes.

Because of this variation in dimorphism, Peters divides *Pt. viridis*, as understood here, into four species, *Pt. viridis*, *eugeniae* (including *lewisii* and *vicinus*), *geelvinkiana*, and *pectoralis* (including *salvadorii*). This is not necessary. All these forms are very closely related and all are geographical representatives, with no overlap or contiguity of ranges. Consequently, since they never meet in the wild, it is impossible to say whether they are species or subspecies ; when there is reasonable doubt it is much more convenient to list such forms as subspecies, so that their close relationship is immediately obvious from their names. Sexual dimorphism is not necessarily a specific character. It is an individual character varying within single populations in some of the Geospizinae (Lack, 1947).

(4) *The purpuratus species-group*

This species-group is the largest and the most difficult to subdivide in the genus. It has been revised recently by Ripley and Birckhead (1942) who have introduced many notable improvements in the arrangement of the various forms. A further consideration of it (Cain, in press) shows that certain alterations to Ripley and

Birckhead's subdivisions are necessary. They omit *Pt. pulchellus* (19) and *Pt. superbus* (15) which also belong to the group (Cain, 1954), and divide the forms into four subgroups, (i) the " old stock," the forms in Australia, New Guinea the North Moluccas, and the Marianas (17, 18, 20, 21), (ii) Subgroup A, the forms from Rarotonga eastward and *Pt. perousii*, (16, 25–28), (iii) Subgroup B, those in the Solomons, New Hebrides, Fiji (*Pt. porphyraceus*), Carolines and Palau Islands (22–24) and (iv) the two Marquesan forms (29, 30) which they think should probably be placed in Subgroup B. The characters given by them as distinctive of Subgroups A and B are inconstant. They were unfortunately unable to see specimens of *Pt. rarotongensis* (25). An examination of specimens in the British Museum (Natural History) shows that it is in every way intermediate in pattern as well as geographically between *Pt. porphyraceus* (24)) (Subgroup B) and *Pt. purpuratus* (27) (Subgroup A), and that the proposed distinction between the two subgroups cannot be upheld. On the basis of this distinction, Ripley and Birckhead suggest that the " old stock " has given rise to two eastward expansions, one producing Subgroup A including *Pt. perousii* (16), the other Subgroup B, to the west of A, which has since spread into Fiji (*Pt. porphyraceus* (24)) and there overlaps with Subgroup A without interbreeding. Subgroup B, they suggest, has also colonized the Marquesas twice (producing *Pt. dupetithouarsii* (30) and *Pt. mercieri* (29)), leaping over the enormous range of Subgroup A to do so.

The abolition of the distinction between Subgroups A and B allows us to recognize that, with the exception of *Pt. perousii* (16) and the Marquesan species (29, 30) all the forms from *Pt. regina* (20) eastward are geographically representative and so closely allied that there is no reason to believe them to be more than the results of a single vast eastward expansion (Cain, in press). *Pt. perousii* (16) does not belong to this superspecies, but forms with *Pt. superbus* (15) a distinct subgroup within the species-group (Cain, 1954). The closest allies of the Marquesan species are *Pt. insularis* (28) on Henderson Island (regarded by Ripley and Birckhead as a subspecies of *Pt. purpuratus* (27)) which appears to be closely related to *Pt. mercieri* (29), and *Pt. purpuratus* (27) which is allied to *Pt. dupetithouarsii* (30). There is no doubt (Mayr, 1940) that the Marquesan species are the result of a double invasion by the same stock. Both, consequently, are geographical representatives of their closest allies, but it is not possible to choose one rather than the other to add to the superspecies, leaving one outside it because of their overlap. Consequently in the classification given above they are placed next to their closest allies and bracketed together as a *doublet*. The same procedure is used for *Pt. pulchellus* (19) and *Pt. coronulatus* (18) for the same reason. The whole of the purpuratus subgroup can then be accurately described as one superspecies with two doublets.

The Henderson Island form, *Pt. insularis* (28) although a geographical representative of all the others in the subgroup, is probably rather more closely allied to a member of the Marquesan doublet (namely *Pt. mercieri* (29)) than to any of the non-overlapping forms. But its relationships are so complex that it is retained here as a single species, since it could probably be considered almost equally well as a subspecies of either *Pt. mercieri* (27) or *Pt. purpuratus* (27). Whatever its detailed relationships, it is certainly a member of the superspecies.

SUMMARY

1. Proposed classifications of the large genus *Ptilinopus* are unsatisfactory, because either they are constructed on the principle that anatomical characters are invariably more important than colour-pattern, or they are really keys. A classification considered to be free from these defects is given.

2. Because of considerable variation in specific characters, it may be impossible to diagnose a very natural group of species. The group is then sufficiently defined by a description of its principal trends of variation, and a list of its contents.

3. Examples are given of the use of the species-group as a convenient informal taxonomic rank, indicating relationships without causing nomenclatorial upheavals.

4. The use of brackets for indicating multiple invasions by closely related stocks is exemplified.

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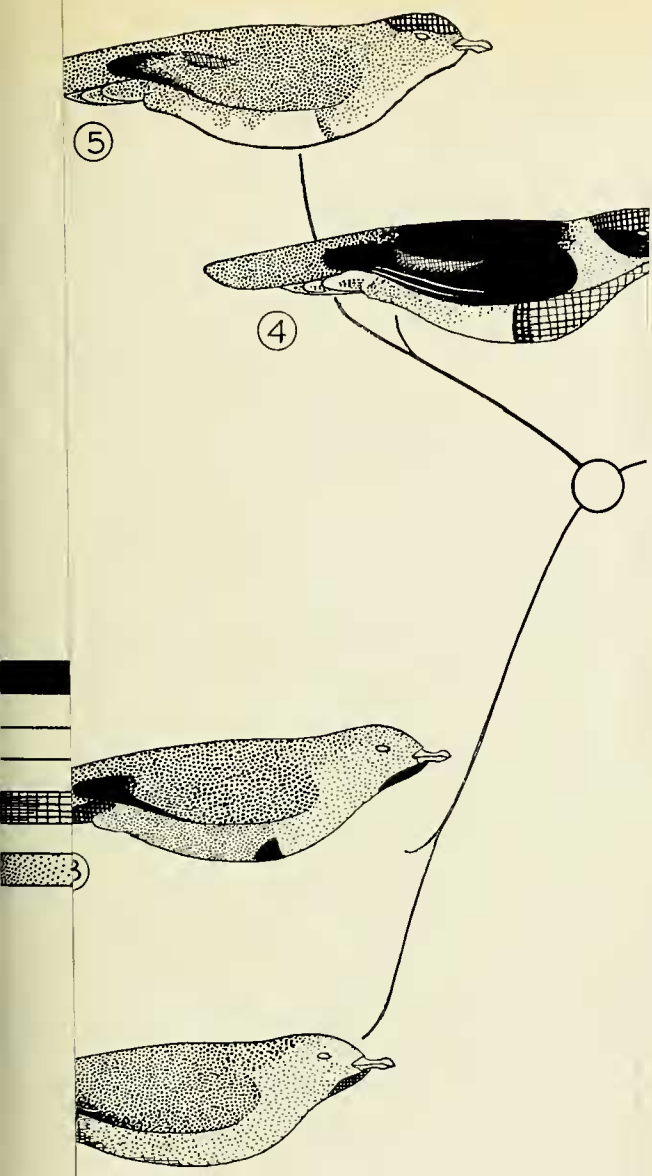

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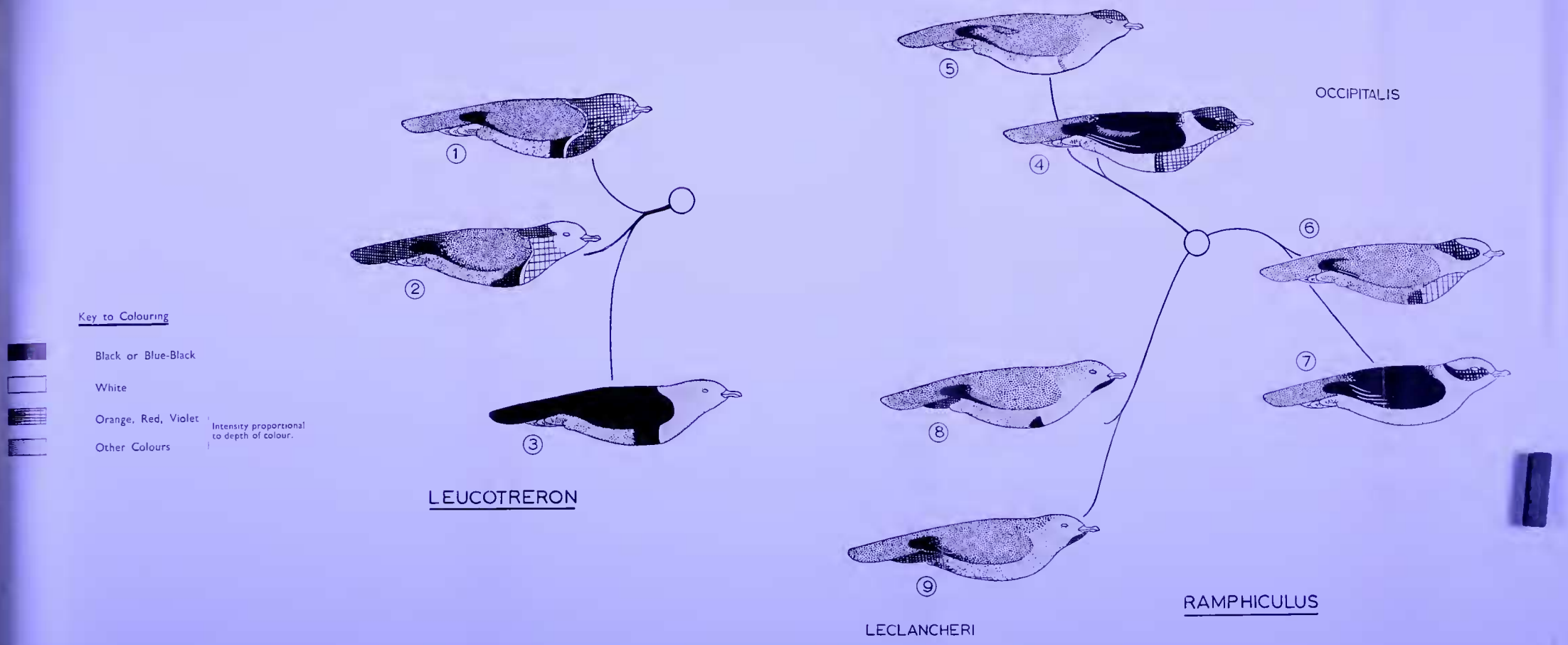
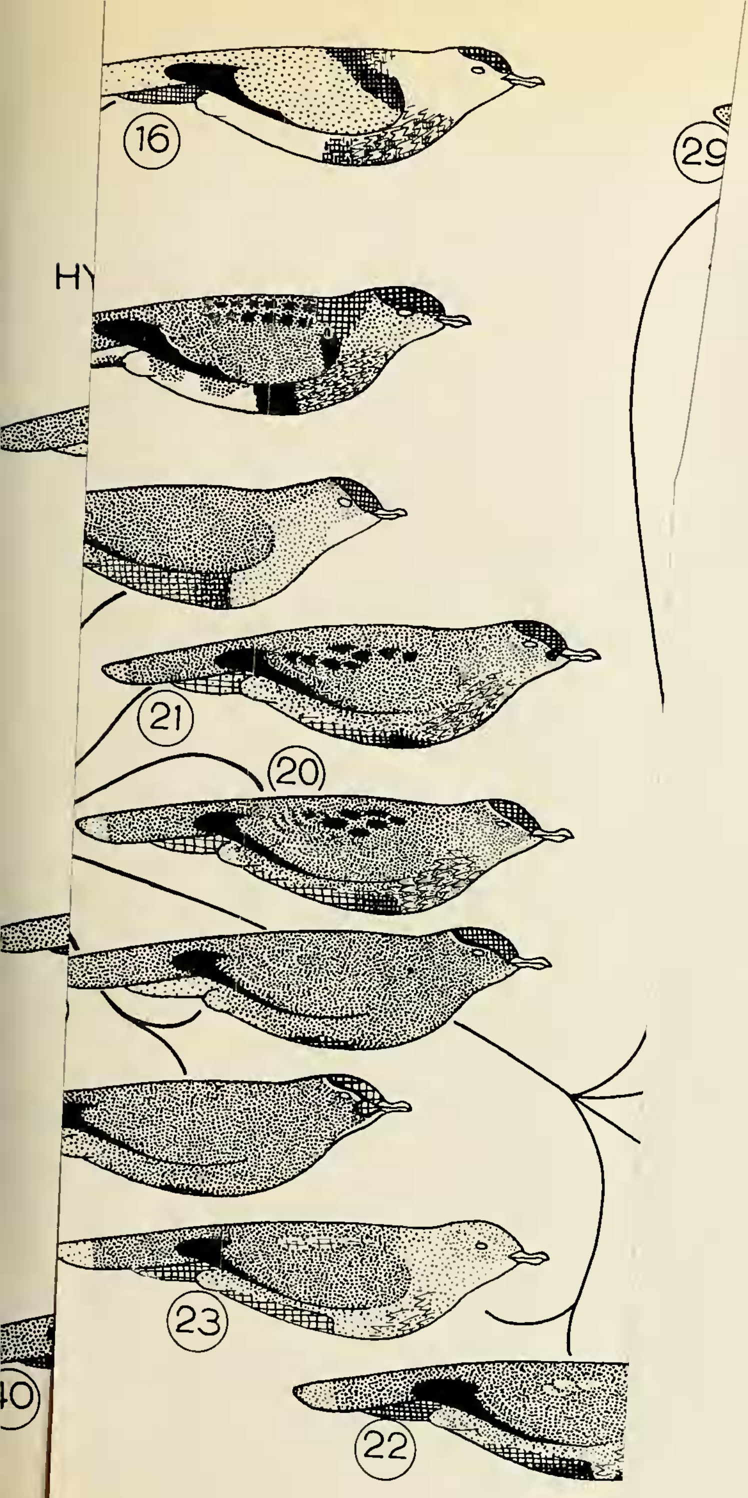

Key to Colouring
Black or Blue-Black
White
Orange, Red, Violet
Other Colours
Intensity proportional to depth of colour.
1
2
3
LEUCOTRERON
5
4
OCCIPITALIS
6
7
8
9
LECLANCHERI
RAMPHICULUS

FIG. 1.


16
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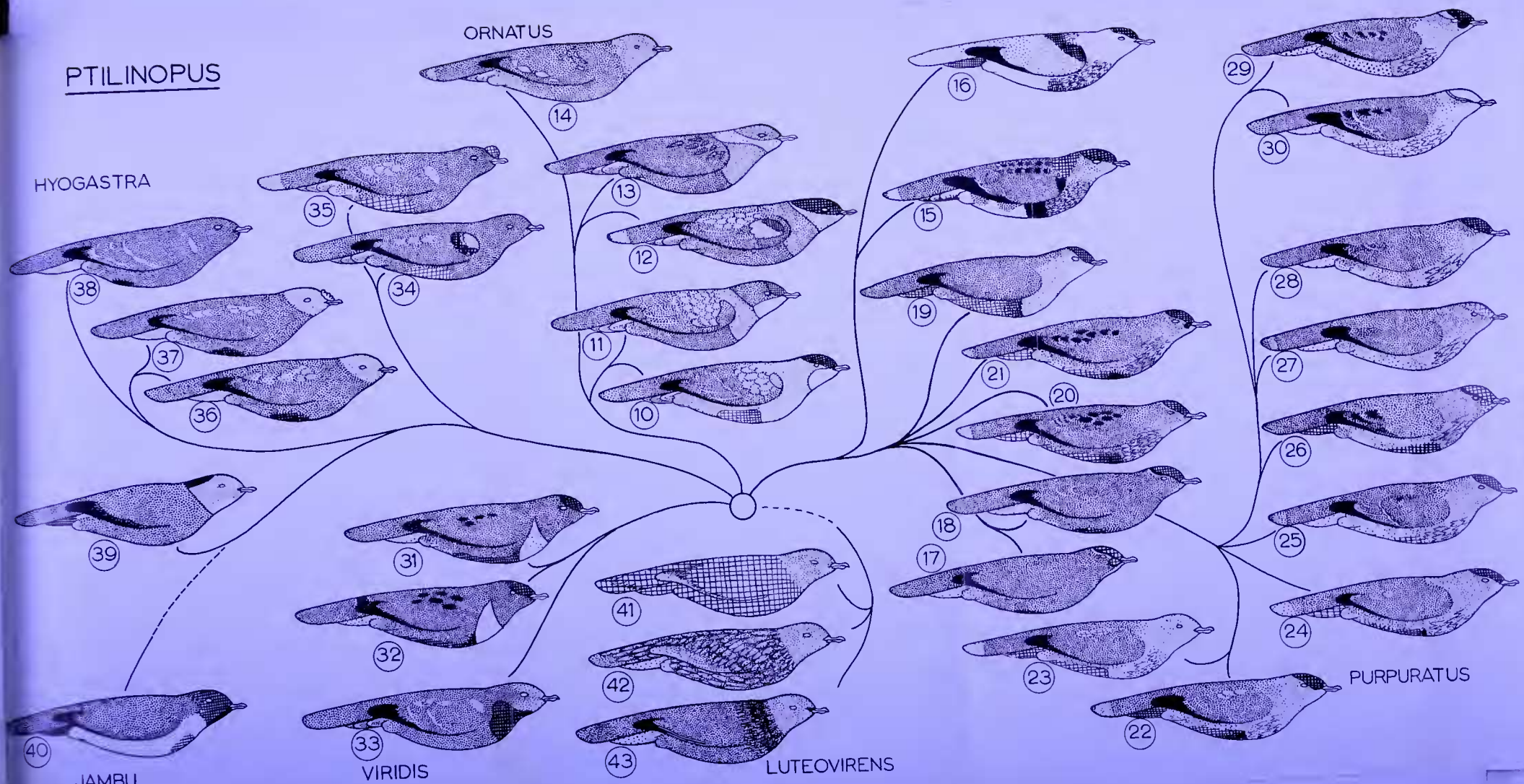
PTILINOPUS
ORNATUS
HYOGASTRA
JAMBU
VIRIDIS
LUTEOVIRENS
PURPURATUS
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FIG. 2.